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SOME FEATURES IN THE ANATOMY OF THE MALVALES.[1]

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In the study of the phylogeny of plants there are certain general principles upon which conclusions are based, among which the law of recapitulation is of the utmost importance. This law in its application to plant anatomy shows that primitive conditions are found in the seedling and in the first annual ring of growth. Furthermore, investigation has shown other primitive regions, viz., the root, the leaf petiole, and the reproductive axis. Experimental work has also demonstrated the value of traumatic regions. Studies in these directions have shown that the root is the most conservative, while the stem is the most progressive region of the plant, and consequently this latter organ loses its ancestral characters sooner than any other. It has further been shown that of these organs, the leaf petiole and reproductive axis are more progressive than the root, but not so much so as the stem, which makes them valuable as localities of transitional tendencies. Lastly, but by no means of the least importance, is the region of injury.

Many examples might be cited in illustration of these general principles taken from the anatomical features of the Conifers, an exceptionally favorable group for studies of this nature, owing to the abundance of fossil material of ancestral forms. One exemplification will serve. Pinus is considered to be the lowest genus of the Abietineae, a group in which resin canals appear normally in the woody cylinder, but in Abies, and other of the Abietineae, resin canals do not normally develop in the wood of the stem, but are found in the xylem of the root and other conservative organs, as well as in traumatic regions, thus illustrating the principles of retention and reversion. Since it has been somewhat generally admitted by competent investigators that the Abietae have been derived from the true pines, or Pineae, the natural inference is, that the conditions found in these conservative regions, just mentioned, may be taken as phylogenetic evidence of ancestral conditions (1). Still further illustrations of evolutionary tendencies in plants are found in Quercus, etc., by anatomical investigation and experiment. Studies of fossil ancestors of Quercus show that the uniseriate ray is primitive. A higher condition is seen where the rays are grouped in clusters to constitute the aggregate ray often found in relation to the leaf-trace. This condition is also present among others of the lower Cupuliferae, namely, Alnus, Carpinus, Corylus, and Betula. In this Angiospermous family, however, the conditions described are often found only in the first annual ring, or more persistently in the seedling, indicating that the aggregate ray is a relatively primitive condition, and consequently of phylogenetic importance (2).

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[1] Contributions from the Phanerogamic Laboratories of Harvard University, No. 66.

Another important anatomical feature is the distribution of wood parenchyma, in regard to which, a somewhat exhaustive investigation of many of the American species of the woody Dicotyledons has established, preliminarily, certain general conditions. The first is where the parenchyma is diffuse, that is, scattered throughout the woody portion of the stem; a second condition is vasicentric, and here the parenchyma is clustered around the vessels; the third mode is that where it is found only at the end of the annual ring, or terminal. That these respective conditions of distribution are of phylogenetic importance has been shown by investigation among the lower Angiosperms. The Casuarinaceae, Fagaceae, Betulaceae, Juglandaceae, Rosaceae, etc., show diffuse parenchyma; while studies of the higher forms, *i. e.*, the Oleaceae, Ulmaceae, Rhamnaceae, Parietales, Leguminosae, Compositae, etc., show vasicentric parenchyma. From these examples it is evident that the diffuse condition is the more primitive, since it is so characteristic of the lower orders, and that vasicentric is more advanced, since it is similarly characteristic of the higher orders. As terminal parenchyma occurs both in the higher and the lower orders of the Dicotyledons, it is evident it is not on the same footing as the other two methods of parenchyma distribution, and investigation has shown this to be the case. Miss Holden (3) obtained the following results in her studies of the Salicales: *Populus balsamifera* L., *nigra* L., *grandidentata* Michx. and *laurifolia* Ledeb. possess normally terminal parenchyma, but in the traumatic and conservative regions, vasicentric parenchyma was found. Similar conditions appeared in *Salix nigricans* Smith, *hookeriana* Barratt, *japonica* Thunb. and *daphnoidea* Vill.; but studies of the root, young stem, and wounded material, revealed also vasicentric parenchyma. In summing up the conditions found in the Salicales mentioned, the normal distribution was terminal, but vasicentric conditions were a feature of primitive regions. An application of the principles of comparative anatomy led to the conclusion that the species of Salix and Populus with terminal parenchyma were derived by reduction from those which possessed vasicentric storage cells, and were, therefore, less primitive species (3). It will be shown later that terminal parenchyma in the Angiosperms, although not in the Conifers, is the result of reduction.

The present article deals with conditions found in certain of the Malvales.

Beginning with the Tiliaceae, figure 1 shows a transverse section of *Tilia americana* L. From this it appears that the wood elements are all thin walled, and the numerous clustered vessels are diffuse. The wood parenchyma is present as thin walled cells extending as tangential bands between the rays, which become broadened in the phloëm region. In the upper portion of the figure alternate layers of hard and soft bast appear, of which the latter is composed of sieve tubes and storage cells. Figure 2 represents a tangential section of the same plant, showing one of the bands of parenchyma, the cells of which are indicated by thin-walled rectangular elements in the central portion of the illustration. A similar section through the first annual ring shows abundant diffuse parenchyma, which gradually becomes reduced to tangential bands in the later rings, shown in figure 1. Figure 2 also represents the numerous diffuse vessels with abundant, spirally arranged bordered pits and tertiary thickenings. However, no indication of fusion of the pits to mere slits, a condition common in the Malvaceae and Sterculiaceae, was found. The two types of rays are similiar to those which Bailey (op. cit.) mentions in his studies of Betula, Carpinus, Ostrya, and Corylus.

Figure 3 shows a transverse section of *Hibiscus tiliaceus* L. of the Malvaceae. Here the wood elements consist of bands of thick and thin-walled cells, alternately arranged between the two types of rays. The thin-walled portion is composed of clustered vessels and fibers, a condition very similar to that found in Tilia. This differs greatly from the thick-walled area, where the absence of vessels is conspicuous, and there is abundant diffuse parenchyma, which appears as thin-walled light and dark cells. The dark appearance of certain cells represents the transverse wall of the wood parenchyma, in which simple pits may often be seen. Figure 4 illustrates a radial section of the same possessed the diffuse type, and therefore, in this respect, represent a high development among the Malvales.

The Javanese species chosen from the Bombaceae, *Durio zibethinus* L., presents very interesting characters. Figure 13 shows a transverse section of a mature branch. Abundant diffuse parenchyma cells, including crystals, are characteristic for the species in addition to the normal type as found in the Tiliaceae. Figure 14, a higher magnification of the same area, shows better the average distribution of parenchyma, the cells of which are distinguished from the fibers by thin walls, simple pits, and crystals. Returning to figure 13, the central portion shows a departure from the normal structure in the presence of an aggregate ray with its included fibers. Figure 15, a radial section from the same material, shows, besides the rectangular parenchyma cells, those which have undergone secondary division to cubical cavities in which crystals are deposited. The aggregate structure of the ray shows even more clearly in a tangential section, figure 16, and in figure 17, a higher magnification of a single ray with its included fibers, which are in the process of transition to parenchyma, as is indicated by the septate condition. Figure 18 is similar to figure 16 except that a leaf-trace is included, thus showing the origin of the aggregate ray. The reason for the gradual transition to the diffuse type can be seen by a careful study of the tangential sections which show that all the included fibers are septate, an indication of transition to normal ray parenchyma without included fibrous elements.

The presence of aggregate rays in an order in which the diffuse type is normal is significant. Reference has already been made to the relative development of rays in which it was stated that the aggregate rays indicate a more primitive condition than those of a diffuse character, which points to the conclusion that, since Durio possesses this type of ray, it represents a more primitive condition than any of the other species of the Malvales described in this paper.

Still further proof of the presence of aggregate rays was presented by serial sections through several annual rings of growth in a stem which showed no indication of having been wounded, which, with the abundance of diffuse parenchyma, may be considered as indicative of primitive conditions. Consequently, so far as the anatomy of the stem is concerned, it is evident that Durio is the most primitive of the Malvales examined, since it still retains the aggregate ray as well as abundant diffuse parenchyma, which conditions are very similar to

American species of Nothofagus, and are shown in figure 11, a transverse section. Wood parenchyma occurs only in a terminal position, and is frequently differentiated from the libriform fibers by the presence of crystals of calcium oxalate. A tangential section through the end of the annual ring, seen in figure 12, shows very clearly parenchyma cells, libriform fibers, and rays. An examination of the parenchyma shows, beside the simple pitting, the difference between ordinary parenchyma and crystal cells; the latter have been derived from the former by further subdivision.

Since the anatomical characters of Elaeocarpus correspond so closely to those found in Aristotelia, especially in respect to the distribution of wood parenchyma, it is evident that these features are the result of similar conditions of reduction.

Terminal parenchyma in the Angiosperms is apparently the result of reduction from ancestral forms in which either vasicentric or diffuse parenchyma was present. This has already been shown to be the case in the Salicales by Miss Holden, where those representatives which normally present only terminal parenchyma retain the vasicentric condition in traumatic and primitive regions, thus illustrating the principles of retention and reversion, respectively. Conditions very similar to those are to be seen in the Fagaceae, in which group, parenchyma occurs normally as cells scattered throughout the wood. Investigation of the aberrant South American representative, Nothofagus, shows only terminal parenchyma in the stem. This genus thus shows similarity, *mutatis mutandis*, to the Salicales investigated by Miss Holden (3).

From a consideration of the evolutionary tendencies in the two above mentioned families, it is evident that those which possess terminal parenchyma have suffered a reduction from more primitive ancestors which showed, in the one case, vasicentric, and, in the other, diffuse parenchyma, and consequently represent more advanced species.

Applying the above mentioned principles of Elaeocarpus and Aristotelia, two species which show terminal parenchyma, it is evident that they have been derived by reduction from more primitive ancestors; and, since the two examples cited show a reversion in recessive regions to the type of parenchyma distribution normally present in the less advanced members of the order, Elaeocarpus and Aristotelia may be considered as having suffered a reduction from ancestors, which possessed the diffuse type, and therefore, in this respect, represent a high development among the Malvales.

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Considering the Malvales as a whole from the morphological standpoint, it is evident that they represent a relatively low order among the Dicotyledons, and that the anatomical data appear to assign to them a position less high than that designated in the Syllabus der Pflanzenfamilien by Engler and Gilg, which places them between the Rhamnales and Parietales, both of which have vasicentric parenchyma, a condition very characteristic of the higher Dicotyledons. It may be stated here that in the investigations carried on in this laboratory, there has never been found a case where vasicentric parenchyma and aggregate rays were coexistent. Therefore, to place a group where aggregate rays occur and vasicentric parenchyma is characteristically absent, between two orders, which show diffuse rays and vasicentric parenchyma, appears to be unjustified.

There is a striking similarity in the morphological conditions found in the Malvales and the lower Dicotyledons in respect to the distribution of parenchyma which resembles that seen in Fagus, Betula, Alnus, Carpinus, and Corylus (all of which normally present diffuse wood parenchyma). In Fagus, however, there is a tendency toward a reduction to a terminal position, as mentioned above as an analogy to the conditions found in Aristotelia and Elaeocarpus. Further, this similarity is no more striking than is that of the ray structure, which, as in the above mentioned species, is normally of the diffuse type, with a tendency toward a reversion to the aggregate condition in Durio, which compares favorably with that found in Betula. Investigation has shown that in *Betula populifolia*, a recognized primitive species, aggregate rays occur normally, but in *Betula alba*, which is more advanced, such rays occur only in the first annual ring, or more persistently in the seedling.

From the study of the anatomical conditions found in the Malvales, it seems probable that they were descended from ancestors which normally possessed diffuse parenchyma and aggregate rays, which characters the tropical genus, Durio, still retains in the normal stem, and consequently appears from the anatomical standpoint to be the most primitive species examined. Without doubt from forms similar to this, the other genera were derived. The aggregate ray gave place to that of the diffuse type, as a result of the transformation of the included fibers to normal ray parenchyma, which, in the other species, takes place in the immediate vicinity of the leaf-trace.

During the gradual transition of the rays to those of a diffuse character, there has been, in some cases, a reduction of the wood parenchyma from the uniform diffuse condition, as seen in Durio and Fremontia, to the Hibiscus type, in which there are thin-walled areas in which the parenchyma is of infrequent occurrence. This process of reduction has reached a higher step in Tilia, where the parenchymatous wood elements occur only as tangential bands, with the exception of the first annual ring, where there is a reversion to the uniform diffuse condition. The climax of this process of reduction is reached in Aristotelia and Elaeocarpus, where it occurs only in a terminal position; and, applying the principles illustrated by Salix and Fagus, it is evident that these two genera represent the least primitive condition since they are the most reduced, and are, therefore, the most advanced, of all the Malvales mentioned in this paper.

SUMMARY AND CONCLUSIONS.

1. The primitive Dicotyledons had apparently diffuse parenchyma and aggregate rays.

2. All the Malvales examined, except Elaeocarpus and Aristotelia, show diffuse parenchyma in varying amounts.

3. Durio presents aggregate rays and diffuse parenchyma, and is therefore, to that extent, the most primitive of the Malvales examined.

4. Elaeocarpus and Aristotelia possess only terminal parenchyma, and therefore represent, in this respect, reduced species.

5. Applying general anatomical principles to the conditions cited above, it is evident that the Malvales came from ancestors possessing diffuse parenchyma and aggregate rays.

In conclusion, I wish to express my sincere thanks to Miss Frieda Cobb for material of Nothofagus; to the Director of the Harvard Botanical Garden for material of the herbaceous forms; and to Professor E. C. Jeffrey for his helpful advice and aid in securing the photomicrographs accompanying this article.

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EXPLANATION OF PLATES IX–XI

FIG. 1. Tilia americana L.: transverse section of normal wood, showing diffuse parenchyma and thin-walled elements. × 200.

FIG. 2. Same: tangential section, showing diffuse parenchyma and rays. × 200.

FIG. 3. Hibiscus tiliaceus L.: transverse section, showing diffuse parenchyma and thick and thin-walled elements. × 200.

FIG. 4. Same: radial section, showing diffuse parenchyma. × 200.

FIG. 5. Fremontia californica Torr.: transverse section, showing diffuse parenchyma and thick-walled wood elements. × 200.

FIG. 6. Same: radial section, showing diffuse parenchyma. × 200.

FIG. 7. Aristotelia DC.: transverse section, showing terminal parenchyma. × 200.

FIG. 8. Same: tangential section through the end of the annual ring, showing terminal parenchyma. × 200.

FIG. 9. Fagus grandifolia Ehrh.: transverse section, showing diffuse parenchyma. × 200.

FIG. 10. Same: radial section, showing diffuse parenchyma. × 200.

FIG. 11. Nothofagus: transverse section, showing terminal parenchyma and crystal cells. × 350.

FIG. 12. Same: tangential section through the end of the annual ring, showing terminal parenchyma and crystal cells. × 200.

FIG. 13. Durio zibethinus L.: transverse section, showing diffuse parenchyma and aggregate rays. × 150.

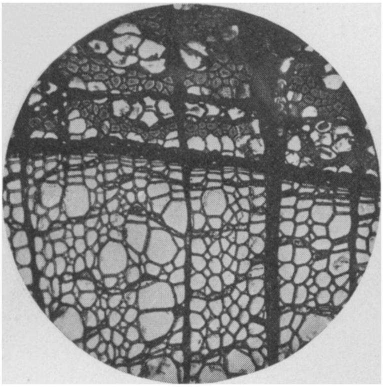
FIG. 14. Same: showing diffuse parenchyma and crystal cells. × 400.

FIG. 15. Same: radial section, showing diffuse parenchyma and crystal cells. × 250.

FIG. 16. Same: tangential section, showing aggregate rays and diffuse parenchyma. × 45.

FIG. 17. Same: showing aggregate ray with included septate fibers. × 120.

FIG. 18. Same: showing aggregate rays and leaf-trace. × 18.



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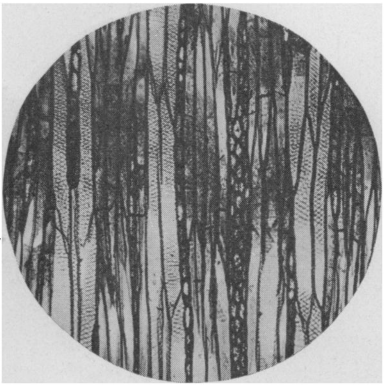

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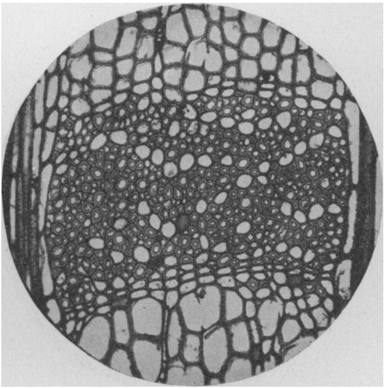

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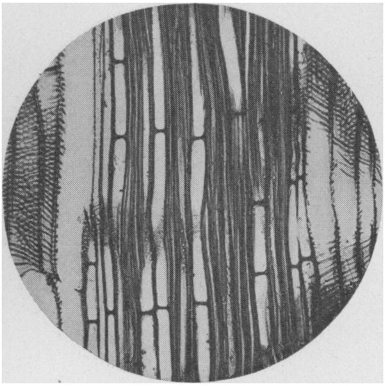

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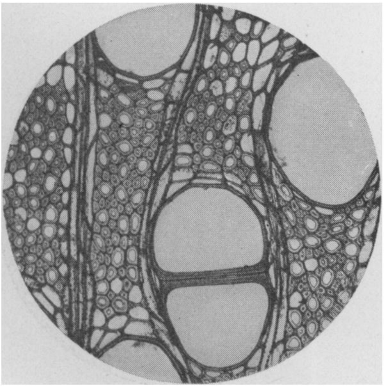

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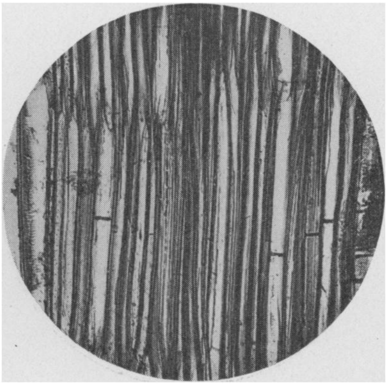

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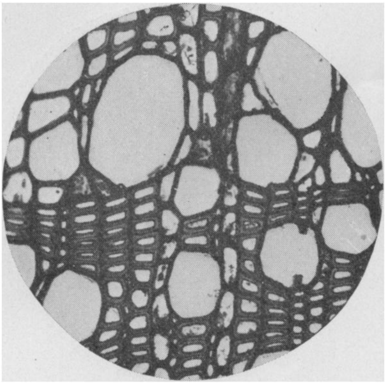

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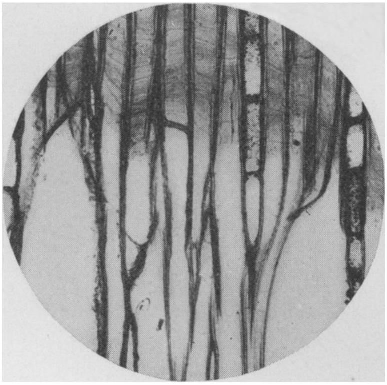

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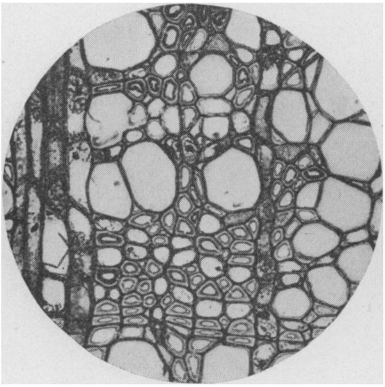

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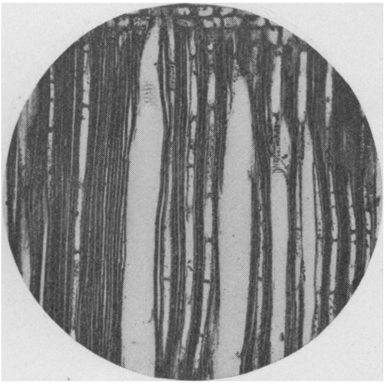

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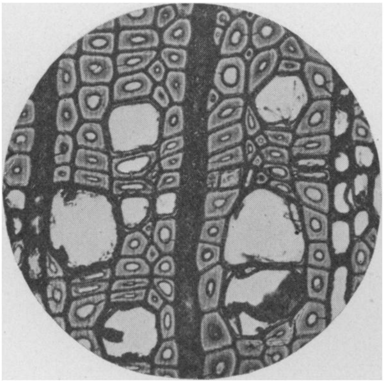

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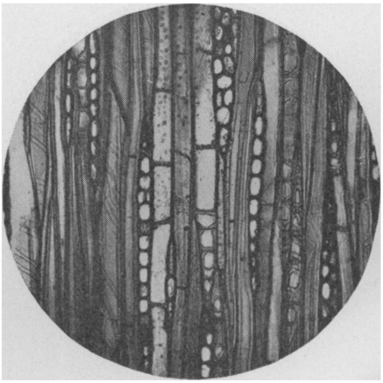

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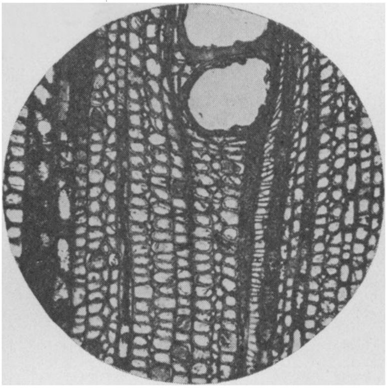

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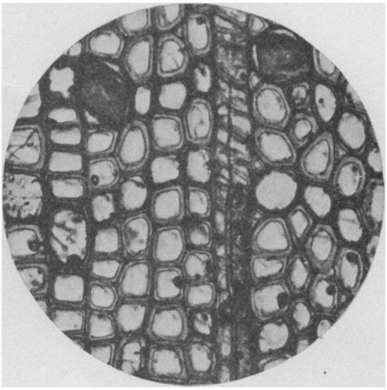

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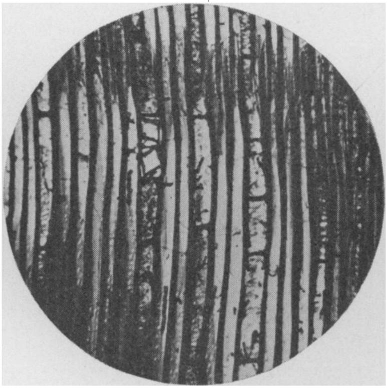

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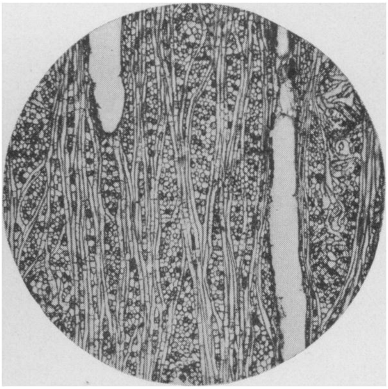

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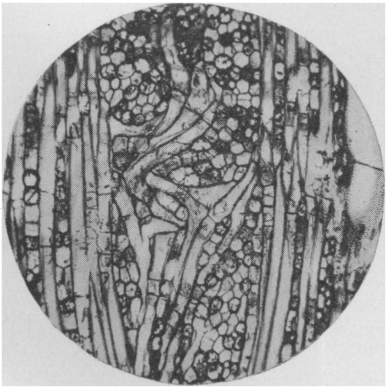

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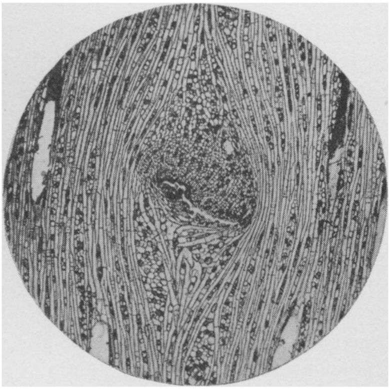

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FORSAITH: ANATOMY OF THE MALVALES.